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Pre-domestication bottlenecks of the cultivated seaweed *Gracilaria chilensis*

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Abstract

Gracilaria chilensis is the main cultivated seaweed in Chile. The low genetic diversity observed in the Chilean populations has been associated with the over-exploitation of natural beds and/or the founder effect that occurred during post-glacial colonization from New Zealand. How these processes have affected its evolutionary trajectory before farming and incipient domestication is poorly understood. In this study, we used 2232 single nucleotide polymorphisms (SNPs) to assess how the species' evolutionary history in New Zealand (its region of origin), the founder effect linked to transoceanic dispersion and colonization of South America, and the recent over-exploitation of natural populations have influenced the genetic architecture of *G. chilensis* in Chile. The contrasting patterns of genetic diversity and structure observed between the two main islands in New Zealand attest to the important effects of Quaternary glacial cycles on *G. chilensis*. Approximate Bayesian Computation (ABC) analyses indicated that Chatham Island and South America were colonized independently near the end of the Last Glacial Maximum and emphasized the importance of coastal and oceanic currents during that period. Furthermore, ABC analyses inferred the existence of a recent and strong genetic bottleneck in Chile, matching the period of over-exploitation of the natural beds during the 1970s, followed by rapid demographic expansion linked to active clonal propagation used in farming. Recurrent genetic bottlenecks strongly eroded the genetic diversity of *G. chilensis* prior to its cultivation, raising important

challenges for the management of genetic resources in this incipiently domesticated species.

KEYWORDS
domestication, genetic bottleneck, genetic resource, phylogeography, Rhodophyceae, SNPs

1 | INTRODUCTION

The domestication process can be seen as a sustained relationship between humans and plants or animals during which these organisms are selected from wild populations and progressively evolve adaptations to agroecological niches (Zeder, 2015). While domestication of terrestrial species started ~10,000 years ago (Zeder, 2015), with more recent "pulses of domestication," including the domestication of most fruit-producing trees (i.e., apples, peaches and almonds) around 4000–3500 years ago (Cornille et al., 2019; Zohary et al., 2012), most marine species have been cultivated for less than a century (Duarte et al., 2007). Seaweeds are among the most recently cultivated and incipiently domesticated organisms. Large-scale seaweed cultivation began about 75 years ago (Valero et al., 2017). Eight species belonging to the genera *Gracilaria*, *Eucheuma*, *Kappaphycus*, *Pyropia*, *Saccharina* and *Undaria* represent the major part of commercially grown seaweed crops and are now showing signatures of phenotypic and genetic divergence from wild populations (Valero et al., 2017). Increasing focus on seaweed cultivation stemmed from the rapid increase in demands of the food and chemical industries that cannot be met by harvesting biomass from natural populations (Buschmann et al., 2001; Hafting et al., 2015; Valero et al., 2017). Population genetic inferences of the domestication history of terrestrial plants have commonly revealed strong genetic bottlenecks due to selective sweeps and/or drift linked to the use of few/local seeds (i.e., Molina et al., 2011), sometimes with a recovery of genetic diversity after domestication as a result of introgressions with wild relatives (i.e., Hufford et al., 2012). The development of seaweed aquaculture can also lead to genetic bottlenecks and the erosion of genetic diversity (brown algae: Guzinski et al., 2018, Zhang et al., 2017; red algae: Guillemin et al., 2008, Hurtado et al., 2019). This reduction has been particularly severe in the case of algal crops propagated vegetatively, with many of the farms established outside of the species native range using a very small number of individuals/biomass for seedling (i.e., *Gracilaria* farms in the northern part of Chile: Guillemin et al., 2008; *Eucheuma* and *Kappaphycus* farms in some 30 countries: Conklin & Smith, 2005; Zuccarello et al., 2006; Chandrasekaran et al., 2008; Halling et al., 2013; Hayashi et al., 2017; Hurtado et al., 2019). Few innovations and investments have been made in Gracilariales and eucheumatoids to steady the loss of the crops' genetic diversity and to preserve genetic resources present in both natural populations and farming facilities (Brakel et al., 2021; Hurtado et al., 2019). This has been associated with rapid crop failure due to loss of strain vigour and the increase in pest, epiphyte and disease susceptibility (Hayashi et al., 2017; Hurtado et al., 2019; Vairappan et al., 2008; Valderrama et al., 2015). There is an urgent need to implement long-term sustainable aquaculture practices to counter the setbacks being experienced.

On top of the problems resulting from current cultivation practices, the status of genetic resources prior to the establishment of farming operations is poorly understood. Most species have been harvested for decades, even centuries, before being cultivated (i.e., *Porphyra/Pyropia* spp. have been traditionally harvested for at least 900 years for their consumption as Nori, and *Undaria pinnatifida* since 1600 to produce Wakame; Valero et al., 2017). How harvesting has affected the population genetic diversity of seaweeds remains largely unknown (Faugeron et al., 2004). On a broader spatiotemporal scale, population dynamics and connectivity have promoted spatial genetic structure that has influenced the success of some breeding strategies. For instance, Asian kelps have experienced population divergence in glacial refugia (Zhang et al., 2015, 2019), that served as a basis for a breeding strategy promoting heterosis, by producing hybrid crosses between divergent populations (Goecke et al., 2020; Hwang et al., 2019; Wang et al., 2020).

Gracilaria chilensis is the main cultivated seaweed in Chile (Buschmann et al., 2017). The species has been an important economic resource in the country since the 1950s–1960s, when intense harvesting of the natural populations began to supply the phycocolloid industry (Buschmann et al., 2008). Over-exploitation led to the collapse of natural populations in the late 1970s and hundreds of farms were created along the Chilean coast to sustain the production. Today, natural populations are found in a relatively narrow range, from the Bio-Bio region (36° S) to Chiloe Island (42.5° S), while farms are operating from Patagonia (43.5° S) to Northern Chile (23° S). The development of farms was initially limited by the difficulty of completing the sexual life cycle. Indeed, *Gracilaria* species have a triphasic life cycle, with diploid tetrasporophytes that release spores after meiosis, haploid male and female gametophytes that produce gametes, and the diploid carposporophyte that produces diploid spores surrounded by the haploid tissue of the maternal gametophyte. To circumvent this constraint, cultivation of *G. chilensis* is based on a very simple system of clonal propagation of cuttings, collected locally or sometimes exchanged among farmers, that are then grown entwined in ropes or planted in sandy or muddy substrates (Santelices & Doty, 1989). This practice has interrupted the sexual life cycle. Currently, farms are dominated by heterozygous diploid individuals with very little spore production (Guillemin et al., 2008), which has been interpreted as a signature of incipient domestication (Valero et al., 2017). Low genetic diversity has been reported in both farms and natural populations, and has been related to

over-exploitation prior to the start of farming operations (Guillemin et al., 2008). However, another possible explanation for this low genetic diversity comes from phylogenetic and phylogeographical evidence that the species has colonized Chile from New Zealand at the end of the last glacial era (Cohen et al., 2004; Guillemin, et al., 2014; Huanel et al., 2020). Indeed, the species is present all around the two main islands of New Zealand and Chatham Island, where most of the genetic diversity is present (Huanel et al., 2020), and at least 11 species of Gracilariales are found (Gurgel et al., 2018; Neill & Nelson, 2019; Preuss et al., 2020). Only *G. chilensis* is found in Chile and the south of Peru. Such transoceanic dispersal, although probably rare, has occurred in several seaweed and invertebrate species (Fraser et al., 2009, 2013; Guillemin et al., 2016). In *G. chilensis*, the founder effect of such transoceanic colonization was probably strong, as evidenced by the detection a single ribosomal or mitochondrial haplotype shared between New Zealand and Chile (Guillemin et al., 2014). Yet, the observation of private alleles in Chilean populations of *G. chilensis* suggests that population expansion after colonization may have restored some level of genetic diversity (Guillemin et al., 2014). However, the poor polymorphism of the markers used so far (ITS in Guillemin et al., 2014 and Huanel et al., 2020; microsatellites in Guillemin et al., 2008) did not allow precise and statistically powerful assessment of the historical demography of *G. chilensis*.

The relative roles of past founder effects and recent overharvesting are not clearly understood and the central question addressed in this study is which of such previous events, either natural or human-driven, were most influential for the genetic basis of algal crops. This study aimed at deciphering the predomestication history of *G. chilensis* using genomic markers. Three main hypotheses were tested: the low genetic diversity found in Chile is the result of (i) the founder effect during the colonization of Chilean coasts; (ii) the overharvesting prior to the onset of aquaculture; or (iii) both events have strongly affected the genetic basis of this algal crop. To do so, we first analysed the spatial structure of the genetic diversity in New Zealand to identify potential source populations. Then we inferred the transoceanic colonization history of Chile and assessed the effect of recent over-harvesting, considering the previous founder effects. Using samples from the whole distribution range of the species, we analysed natural populations from the native area (i.e., New Zealand) and natural and cultivated populations from Chile and Peru, using RADseq markers.

2 | MATERIAL AND METHODS

2.1 | Sampling

Samples were collected across the entire distributional range of *Gracilaria chilensis* in the Pacific Ocean (Guillemin et al., 2008, 2014; Robitzch et al., 2019; Huanel et al., 2020), including North and South Islands of New Zealand, Chatham Island, and the south of Peru and Chile (Figure 1, Table 1; Table S1). Samples were collected from both rocky shores (i.e., attached individuals resulting from spore settlement, and therefore from sexual reproduction) and soft bottoms (i.e., free-floating thalli propagating vegetatively) when available (Table S1). A total of 687 individuals of *G. chilensis* were sampled, including 439 samples from 22 populations in New Zealand and Chatham Island, eight samples from the only population recorded in Peru and 240 samples from 13 Chilean populations (Table S1). In New Zealand, two species of *Gracilaria* are found in sympatry, *G. chilensis* and *G. transtasmanicum*, that are morphologically indistinguishable in the field (Preuss et al., 2020). The species identity of all samples from New Zealand was corroborated using the molecular diagnostic tool developed by Huanel et al. (2020). The ploidy of each mature individual was determined in the field by direct observation, as well as examination of reproductive structures under a binocular microscope, while amplification of sex molecular markers (Guillemin et al., 2012) was used for the vegetative individuals.

2.2 | DNA extraction and ddRADseq library preparations

Genomic DNA was extracted using a NucleoSpin Plant II (Macherey Nagel), quantified using a Picogreen assay kit (Molecular Probes, EEUU) and normalized to a standard concentration of 2.5 ng μl^{-1}. A double-digest restriction site-associated DNA (ddRAD) library was obtained using the methodology proposed by Peterson et al. (2012) with slight modifications. Briefly, the genomic DNA was digested with *Hha*I and *Pst*I. The samples were amplified using Illumina indexed primers following the standard protocol for multiplexing of Illumina. The combination of 24 different adapters and 12 primers allowed the multiplexing of 288 individuals per library. All individuals were then mixed to equimolar concentration and the DNA fragments were filtered to 400–800 bp with a Pippin Prep (Sage Science). Paired-end sequencing was conducted on an Illumina Hiseq2500 using Rapid Run option at Fasteris.

2.3 | De novo assembly and filtration

The libraries were demultiplexed using the *process_radtags* module in STACKS version 2.4 (Catchen et al., 2011). Reads with low quality value (i.e., Phred score of 10) or with ambiguous barcodes were removed. The de novo assembly was performed in STACKS version 2.4 (Catchen et al., 2011), using the default parameters except for the number of mismatches allowed between stacks within individuals (*–M*), and the number of mismatches allowed between individuals for a given stack (*–n*), which were both set at 4 (parameters chosen following the optimization procedure described in Paris et al., 2017). Using the *population* module, only the first single nucleotide polymorphism (SNP) per locus was retained. SNPs characterized by $H_O > 0.50$ and minor allele frequency MAF < 0.02, present in less than 60% of the individuals ($-r = 0.6$) and in fewer than 35 of the 36

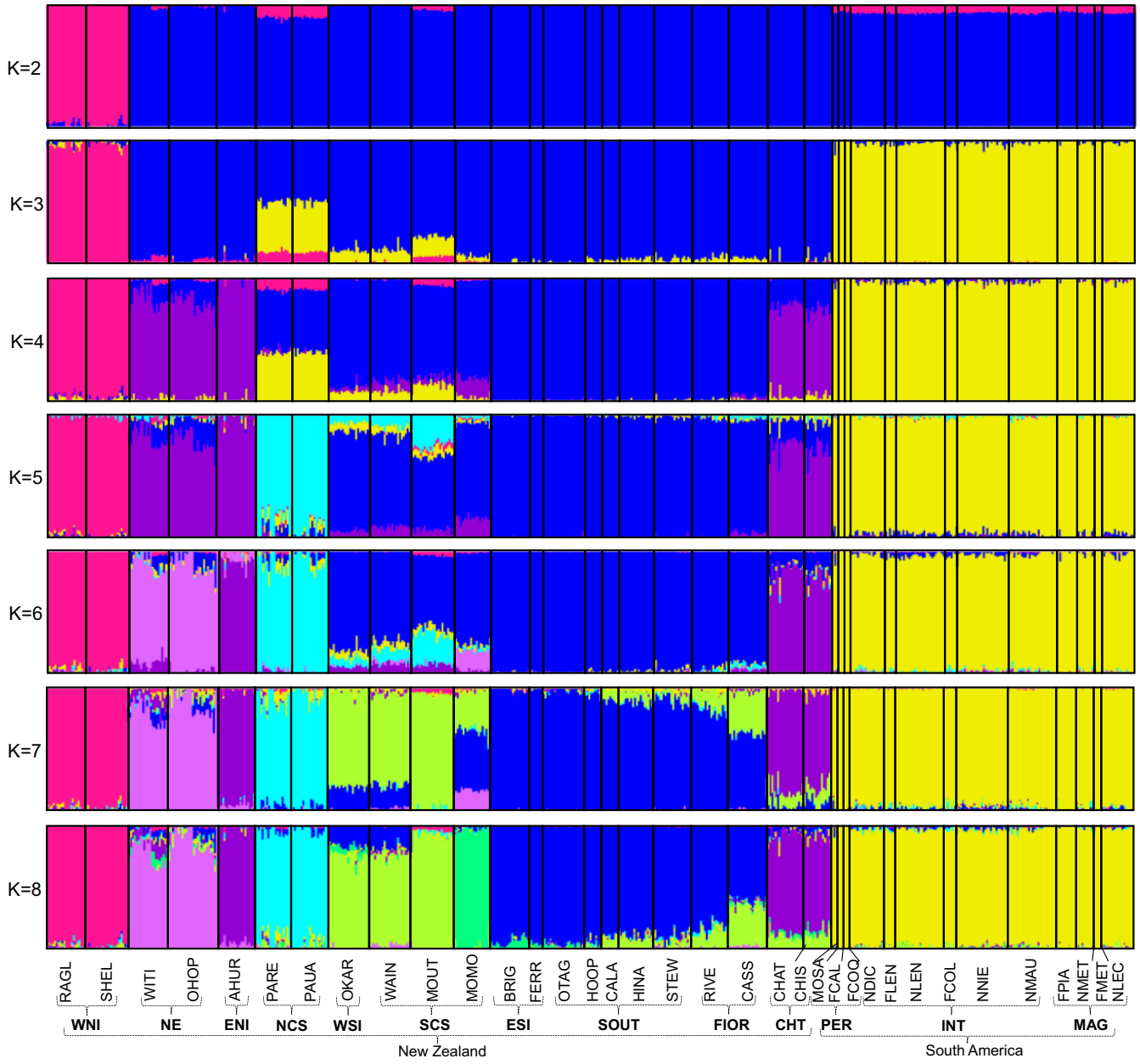


FIGURE 1 Bar plot representing *Gracilaria chilensis* individual genetic cluster assignment from the R package "LEA" with $K = 2$ to $K = 8$. Clones were not considered in the analysis. Codes for localities and bioregions are as in Table 1 and table S1.

populations ($-p = 35$) were discarded. Resulting genotype data were exported as a vcf file and converted into the different file formats necessary for the following analyses using the program PGDSPIDER version 2.1.1.5 (Lischer & Excoffier, 2012).

We also verified the ploidy (diploid vs. haploid) assigned a priori by direct observation and sex markers using the observed heterozygosity (H_O); all individuals were ordered from the lowest to the highest values of H_O in each population sampled and the values of putative haploid and diploid individuals were compared manually with the assigned ploidy ($H_O = 0$ is expected for all haploid individuals when no paralogues are present). Noncongruent H_O values were observed for 19 (2.7%) individuals over the 687 sequenced and the ploidy of these individuals was corrected (Figure S1). The ploidy of 50 vegetative individuals for which sex markers did not amplify was directly deduced from the H_O values (Figure S1).

Finally, putative paralogues were identified as the loci for which H_O was higher than 0 in the corrected set of haploid individuals and were then removed from the data.

In the final data set, haploids were artificially diploidized and appear as homozygous for all loci.

2.4 | Clonal membership assignment

To remove clonal replicates from the data set, clone assignment was performed for each population with the software GENODIVE version

TABLE 1 Summary of genetic diversity obtained in each bioregion included in the study using 2232 SNPs

Country	Bioregion (code)	*N*	*Na*[a]	N_e[a]	%*P*	H_E[a]	*D*	Apriv
New Zealand		*t* = 439	1.12 (<0.01)	1.05 (0.04)	13.17	0.03 (0.02)	0.94	97
	West Coast North Island (WNI)	*t* = 43	1.20 (0.05)	1.07 (<0.01)	30.51	0.05 (<0.01)	1	24
	North Eastern (NE)	*t* = 47	1,27 (0.03)	1.13 (0.01)	35.89	0.08 (<0.01)	1	24
	East Coast North Island (ENI)	*t* = 20	1.20 (<0.01)	1.02 (<0.01)	22.49	0.03 (<0.01)	0.95	25
	North Cook Strait (NCS)	*t* = 40	1.26 (0.02)	1.10 (<0.01)	31.09	0.07 (<0.01)	0.95	0
	West Coast South Island (WSI)	*t* = 22	1.03 (<0.01)	1.01 (<0.01)	2.96	0.01 (<0.01)	1	7
	South Cook Strait (SCS)	*t* = 63	1.12 (0.05)	1.04 (0.04)	31.59	0.02 (0.02)	1	10
	East Coast South Island (ESI)	*t* = 38	1.06 (0.02)	1.03 (0.01)	7.53	0.02 (<0.01)	0.71	0
	Southern (SOUT)	*t* = 92	1.05 (0.02)	1.02 (0.01)	10.66	0.02 (<0.01)	0.90	7
	Fiordland (FIOR)	*t* = 40	1.05 (0.03)	1.02 (0.02)	8.96	0.02 (<0.01)	0.98	0
	Chatham Islands (CHT)	*t* = 34	1.12 (<0.01)	1.05 (<0.01)	7.44	0.03 (<0.01)	0.95	0
South America		*t* = 248	1.07 (0.03)	1.04 (0.02)	6.60	0.02 (0.01)	0.60	0
	Peruvian bioregion (PER)	*t* = 34	1.05 (<0.01)	1.03 (<0.01)	9.05	0.02 (<0.01)	0.26	0
	Intermediate Area (INT)	*t* = 145	1.06 (0.2)	1.03 (0.02)	10.08	0.02 (<0.01)	0.68	0
	Magellanic Bioregion (MAG)	*t* = 69	1.08 (0.02)	1.06 (<0.01)	9.50	0.03 (<0.01)	0.61	0
Total		*t* = 687	1.23 (<0.01)	1.08 (<0.01)	10. 62	0.06 (<0.01)	0.82	97

Note: Bioregions follow the New Zealand Coastal Biogeographic Regions Classification map (available at https://www.doc.govt.nz/documents/conservation/marine-and-coastal/marine-protected-areas/coastal-marine-habitats-marine-protected-areas.pdf), and the Peru–Chile biogeographical classification of Camus (2001). For details about genetic diversity estimated in each locality sampled in the South Pacific Ocean, see Table S1.

Na: mean number of alleles, N_e: effective number of alleles, %*P*: percentage of polymorphic loci, H_E: expected heterozygosity, *D*: proportion of different genotypes, Apriv: number of private alleles.

[a]Standard deviation in parentheses.

3.0 (Meirmans, 2020). GENODIVE uses the genetic distance calculated between each pair of samples to define an assignment threshold that indicates the maximum dissimilarity allowed between two individuals to be considered as clones. We explored thresholds of 5, 6, 8, 10 and 11 mismatches between genotypes to assign clones in the complete data set and selected the highest possible threshold that does not identify clones in individuals attached to hard substratum (i.e., individuals issued from sexual reproduction and spore settlement; Guillemin et al., 2008). Analyses were performed independently for diploids and haploids.

2.5 | Genetic diversity

Genetic diversity was evaluated for all populations and bioregions using various genetic diversity indices: mean number of alleles (*Na*), effective number of alleles (N_e), percentage of polymorphic loci (%*P*), expected heterozygosity (H_E), observed heterozygosity (H_O), number of private alleles (Apriv) and fixation index (F_{IS}). All indices were calculated using GENALEX version 6.5 (Peakall & Smouse, 2006). The proportion of different genotypes was calculated as $D = MLG/N$, where MLG was the number of distinct multilocus genotypes and *N* the total number of studied individuals (Ellstrand & Roose, 1987). Student *t* tests were performed to test for significant differences in genetic diversity (*Na* and %*P*) between the New Zealand and South American *G. chilensis* populations after data transformation using the boxcoxmix package in R STUDIO version 1.2.1335 (R Core Team, 2019).

2.6 | Population structure analysis

Genetic structure in *G. chilensis* throughout the Pacific Ocean was characterized using four approaches. First, we estimated pairwise F_{ST} in ARLEQUIN version 3.5 (Excoffier & Lischer, 2010), adjusting the *p*-values using a false discovery rate (FDR; Benjamini & Hochberg, 1995). F_{ST} values were estimated using only diploid individuals. Second, we estimated the number of genetic clusters (*K*) and the admixture coefficient for each individual, using an analysis of ancestral population assignment available in the package "LEA" in R. The number of ancestral populations tested ranged from $K = 1$ to $K = 36$ (10 repetitions), and the best *K* was selected based on the cross-entropy criterion. Third, a principal component analysis (PCA) was conducted using the function *pca* of the package "LEA" (Frichot & François, 2015). Finally, a phylogenetic network was reconstructed with the algorithm Neighbour-Net, implemented in SPLITSTREE version 4.14.1 (Kloepper & Huson, 2008). The matrix of genetic distances was calculated using uncorrected distances (*Uncorrected_P*) and ignoring the missing data. For the population assignment by LEA, the PCA and Neighbour-Net analyses, haploids and diploids were analysed jointly.

2.7 | Inferring trans-Pacific colonization scenarios

To determine the colonization scenarios most compatible with the observed SNP variation, we first used explicit model comparisons in the program DIYABC-RF (Collin et al., 2021). We examined the most probable origin and route of colonization for Chatham Island and South America from New Zealand. Based on our population structure analyses (PCA), we considered the existence of only five major genetic groups for the DIYABC-RF analyses, namely Northeast coast of North Island (N_1; NE and ENI, Table 1), Northern Cook Strait (N_2; NCS), South Island (N_3; WSI, SCS, ESI, SOUT and FIOR, Table 1) and Chatham Islands (N_4; CHT) in New Zealand, and Chile (N_5). A subsample of 34–37 individuals (including both haploids and diploids characterized by less than 2% of missing data), selected randomly after discarding clones and representing equally all populations assigned to a genetic group, was used as representative of each genetic group. The population of Peru, previously reported as completely clonal (Robitzch et al., 2019), was not included. Likewise, populations from the west coast of North Island, extremely divergent from the rest of the *G. chilensis* sampled (see Results), were not included.

To reduce computational efforts, the choice of the best scenario was made in two steps. First, we defined three groups of competing colonization scenarios. The first group of scenarios involved a common New Zealand origin for both Chatham Island and Chile to test different possible origins (Group 1, three scenarios: Sc1, Sc2 and Sc3; Figure S2). In the second group of scenarios, the colonization followed a stepping-stone process from New Zealand to Chatham Island and then Chile (Group 2, three scenarios: Sc4, Sc5 and Sc6; Figure S2). The third group of scenarios inferred two independent origins of colonization for Chatham Island and Chile (Group 3, six scenarios: Sc7–Sc12; Figure S2). Following Guillemin et al. (2014), the time of colonization from New Zealand to Chatham Island was set as older than that from New Zealand to Chile and we assumed the existence of a bottleneck associated with each founding event. The prior distributions of historical and demographic parameters are described in Table S2. Training sets included 20,000 and 100,000 simulated data sets per scenario for the scenario choice and parameter estimation steps, respectively, as suggested (Collin et al., 2021). Within each group of colonization scenarios, the most likely scenario was identified using a random forest (RF) tree-based classification method. The RF classifier was constructed using 1000 trees per scenario group and the scenario receiving the most votes over all trees was selected. The global and local error rates were estimated by RF regression and used to calculate the posterior probability of the selected scenario (Pudlo et al., 2016). In a second round of scenario testing, the best scenario of each group was kept, and these three remaining scenarios were compared using the same method as described above.

We estimated the posterior distributions of demographic parameters under the best scenario and the precision of each parameter estimation by computing the median as point estimates for each parameter, a 90% credibility interval for each point estimate, and global and local accuracy indices using the approach developed by Raynal et al. (2019). A total of 10,000 bootstrap samples, randomly chosen from the 100,000 simulated data sets, were used for parameter estimation. These analyses were replicated 10 times.

To evaluate the existence, magnitude and direction of gene flow during the trans-Pacific colonization, the DIYABC-RF analyses were complemented by Diffusion Approximations for Demographic Inference (δaδi) analyses (Gutenkunst et al., 2009). Since DIYABC-RF analyses supported a distinct origin for Chatham Island and South America from New Zealand (see Results for more details), we independently evaluated six alternative 2D models to determine the optimal scenario for the colonization of Chatham Island (N_4) from the Northeast coast of North Island (N_1) and of Chile (N_5) from the North Cook Strait (N_2). We used the script easySFS.py (available at https://github.com/isaacovercast/easySFS) to generate a joint-site frequency spectrum (SFS) for N_4 and N_1 and for N_5 and N_2. The seven alternative 2D models followed the analysis pipeline of Portik et al. (2017): (i) founder effect with no migration, (ii) founder effect with constant symmetric migration, (iii) founder effect with constant asymmetric migration (i.e., a higher gene flow from the region of origin to the colonized area), (iv) divergence with ancient symmetric migration, (v) divergence with ancient asymmetric migration, (vi) allopatric divergence without migration, and (vii) divergence with constant asymmetric migration. A visual representation of the demographic models is presented in Figure S3. The model optimization routine was performed using the Nelder–Mead method following the pipeline (Optimize_Functions.py) implemented by Portik et al. (2017). We used four rounds of parameter optimizations with [10, 20, 30, 40] replicates and [5, 20, 125, 200] maximum iterations per round, respectively. The most likely model for each data set (i.e., N_4–N_1 and N_5–N_2) was chosen based on the lowest Akaike information criterion (AIC) score.

To estimate the timing of demographic events we used a mutation rate of 1×10^{-7} (mutation rate inferred for *Arabidopsis*; Bashir et al., 2014) in δaδi. No mutation rate for SNPs is available in red algae. The *Arabidopsis* mutation rate was chosen considering that red algae, jointly with Chloroplastida (a lineage including green algae and land plants) and glaucophytes, form the supergroup Archaeplastida (Burki, 2014). In DIYABC-RF, SNPs do not require mutation model parameterization, and the algorithm of Hudson (2002) was used for all biallelic polymorphic loci as recommended by the authors (Collin et al., 2021). The timing—in years—of demographic events was estimated using a generation time of 1.5 years (following results obtained for population dynamics in *G. chilensis*; Vieira et al., 2021).

2.8 | Testing for scenarios of multiple bottlenecks in Chile

We tested whether Chilean populations of *G. chilensis* passed through simple or multiple bottlenecks prior to the establishment of seaweed farms, including an old founder event linked to the colonization from New Zealand and a more recent demographic bottleneck associated with over-exploitation. We compared four scenarios using DIYABC-RF:

(i) a stable demographic history over time in Chile, (ii) the existence of an old bottleneck associated with the founder event, (iii) the existence of a recent bottleneck linked to anthropogenic impacts, and (iv) the existence of both old and recent bottlenecks in Chile. The Chilean population was rooted in the New Zealand source population identified from the trans-Pacific inferences. Parameter prior distributions are shown in Table S3 and a graphic representation of the four scenarios tested is given in Figure S4. For RF analyses, model choice and estimation of posterior distributions of demographic parameters, we followed the protocols described above.

The DIYABC-RF analysis was complemented with a δaδi analysis (Gutenkunst et al., 2009) by testing between various 1D models of potential historical demographic changes affecting the Chilean population. We examined the following five possibilities: (i) constant population size model, (ii) two-epochs with instantaneous size change, (iii) two-epochs with exponential growth, (iv) two-epochs with instantaneous size decline followed by exponential growth (i.e., bottle-growth) and (v) three-epochs with instantaneous size change (i.e., variation in population size occurred twice, once in a remote past and once in a more recent past). The most likely model for each data set was chosen based on the lowest AIC. As above, for δaδi analyses, timing was estimated using a generation time of 1.5 years (Vieira et al., 2021) and a mutation rate of 1×10^{-7} (Bashir et al., 2014).

3 | RESULTS

An average of 2.5 million reads per individual (ranging from 696,000 to 4,500,000 reads) were obtained for the 687 *Gracilaria chilensis* samples. After removing low-quality reads, 1.8 billion reads were retained across all samples. On average, RAD loci were of 132 bp in length and the individual depth coverage was of 36.8 reads per locus ($\pm16.6SD$). The SNP data set after de novo assembly and filtering contained 2232 biallelic SNPs.

3.1 | Clonal diversity and genetic diversity

The results obtained in GENODIVE, based on thresholds ranging from five to 11, identified from 24 to 30 repeated genotypes, respectively, in our data set. Whatever the threshold used, the number of clones (i.e., ramets) of a repeated genet detected in each population was highly consistent (Figure S5) and we therefore set the threshold distance to five for both diploids and haploids for further analyses. Of the 24 repeated genotypes detected, 11 were from New Zealand and 13 from South America, none of which were shared. Over a total of 150 clones detected with the threshold distance of five (Figure S5), 111 clones (74%) were identified in Peru and Chile and 39 (26%) in New Zealand. The majority of clones were free-floating thalli growing on sand or mud (Peru and Chile: 103 of 111, 93%; New Zealand: 31 of 39, 80%). These results are consistent with the higher number of different genotypes observed in attached sexual populations (New Zealand: $0.95<D<1.0$; South America: $0.75<D<1.0$) than in floating ones (New Zealand: $0.38<D<1.0$; South America: $0.14<D<0.80$) (Table S1). The differences between both types of population are more substantial in Chile where asexual reproduction in floating populations was actively promoted by the vegetative propagation by farmers (Table S1). Within each population, only one sample of each clonal genotype was retained for further analyses of genetic structure (the data set without clones includes 263 haploids and 308 diploids).

The mean number of alleles and percentage of polymorphic alleles were higher in New Zealand than South America (Na = 1.12 and 1.07, t = 2.35, p = .03; $\%P$ = 13.17 and $\%P$ = 6.60, t = 2.71, Student t test p = .01, values are given for New Zealand and South America, respectively, Table 1; Table S1). In New Zealand, the highest genetic diversity was observed in the northeast coast of North Island (North Eastern; NE: Na = 1.27; $\%P$ = 35.89) followed by the rest of the bioregions of North Island and the South coast of Cook Strait (WNI, ENI, NCS and SCS: $1.12<Na<1.26$; $22.49<\%P<31.59$). The diversity of New Zealand bioregions located south of 41°S on the South Island and Chatham Island are similar to that encountered in South America (WSI, ESI, SOUT and FIOR: $1.03<Na<1.06$; $2.96<\%P<10.66$; $0.01<H_E<0.02$; CHT: Na = 1.12; $\%P$ = 7.44; H_E = 0.03). These results are consistent with the number of private alleles detected in our data set, for which the highest values were observed in the West Coast North Island, the North Eastern and the East Coast North Island (Apriv = 24; 24 and 25 for WNI, NE and ENI, respectively; Table 1; Table S1).

F_{IS} values were negative in all New Zealand populations except Ohope. In Chile, attached (sexual) populations had values close to 0 ($-0.12<F_{IS}<0.01$; Table S1), except for Metri (NMET: F_{IS} = −0.50). Contrastingly, floating (clonal) populations had strongly negative F_{IS} values when compared with attached (sexual) ones (i.e. $-0.02<F_{IS}<-0.21$), the most extreme values being observed in Chilean farms ($-0.21<F_{IS}<-0.72$).

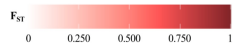
3.2 | Population differentiation and genetic structure

Strong and significant differentiation was detected among populations, except for a few pairs of populations located in Chile (Table 2). The highest F_{ST} values were observed separating populations of Shelly Beach and Raglan sampled in the West Coast North Island (WNI) from the rest of *G. chilensis* ($0.88<F_{ST}<0.96$; Table 2). Pairwise F_{ST} values were smaller when comparing populations from Chatham Island (CHT) with the North Eastern (i.e., NE, Whitianga and Ohope, $0.57<F_{ST}<0.65$) than with the rest of the New Zealand samples. The lowest pairwise F_{ST} values between Chilean populations and populations from New Zealand were observed for the North Cook Strait (i.e., NCS, Paremata and Pauatahanui, $0.55<F_{ST}<0.74$).

The Δ cross-entropy method implemented in LEA suggested the existence of eight clusters as the most likely population structure (Figure S6). At K = 2, the Shelly Beach and Raglan populations

TABLE 2 Pairwise genetic differentiation (measured by F_{ST}) between 35 *Gracilaria chilensis* localities and estimated using 2232 SNPs. Significant values, estimated using a false discovery rate, are shown in bold

Bioregion		NWI		NI		ENI	NCS		WCSI	SCS			ECSI		SOUT					FIOR		CHT		PER		INT								MAG				
Population		SHEL	RAGL	WITI	OHOP	AHUR	PARE	PAUA	OKAR	WAIN	MOUT	MOMO	BRIG	FERR	STEW	CALA	HINA	OTAG	HOOP	CASS	RIVE	CHIS	CHAT	FCAL	FCOQ	NDIC	FLEN	NLEN	FCOL	NNIE	NMAU	FPIA	NMET	FMET	FCHA	NLEC
NWI	RAGL	0.321																																			
NI	WITI	0.890	0.896																																		
	OHOP	0.900	0.905	0.357																																	
ENI	AHUR	0.935	0.935	0.624	0.681																																
NCS	PARE	0.896	0.900	0.593	0.630	0.760																															
	PAUA	0.903	0.906	0.621	0.653	0.776	0.025																														
WCSI	OKAR	0.963	0.958	0.678	0.695	0.873	0.742	0.758																													
SCS	WAIN	0.946	0.944	0.588	0.607	0.806	0.652	0.672	0.678																												
	MOUT	0.921	0.923	0.590	0.612	0.767	0.591	0.618	0.708	0.486																											
	MOMO	0.953	0.950	0.629	0.665	0.854	0.744	0.760	0.899	0.785	0.736																										
ECSI	BRIG	0.948	0.946	0.605	0.642	0.814	0.704	0.723	0.814	0.647	0.665	0.791																									
	FERR	0.943	0.942	0.574	0.615	0.804	0.679	0.701	0.839	0.660	0.654	0.801	0.043																								
SOUT	STEW	0.952	0.949	0.604	0.647	0.825	0.699	0.718	0.825	0.660	0.673	0.807	0.534	0.572																							
	CALA	0.943	0.941	0.537	0.579	0.804	0.635	0.660	0.859	0.613	0.607	0.819	0.478	0.517	0.327																						
	HINA	0.947	0.944	0.566	0.596	0.815	0.650	0.672	0.844	0.607	0.620	0.843	0.559	0.583	0.557	0.470																					
	OTAG	0.951	0.949	0.598	0.624	0.824	0.675	0.695	0.816	0.606	0.637	0.834	0.574	0.595	0.553	0.467	0.004																				
	HOOP	0.955	0.951	0.611	0.634	0.837	0.692	0.710	0.835	0.655	0.666	0.846	0.616	0.650	0.602	0.569	0.489	0.462																			
FIOR	CASS	0.949	0.947	0.596	0.620	0.818	0.661	0.679	0.778	0.558	0.617	0.806	0.585	0.599	0.560	0.506	0.394	0.378	0.457																		
	RIVE	0.957	0.954	0.628	0.649	0.844	0.701	0.718	0.844	0.639	0.660	0.860	0.707	0.735	0.726	0.743	0.724	0.698	0.732	0.601																	
CHT	CHIS	0.943	0.942	0.630	0.659	0.764	0.738	0.755	0.824	0.738	0.723	0.813	0.772	0.766	0.779	0.754	0.759	0.768	0.780	0.757	0.799																
	CHAT	0.936	0.936	0.573	0.606	0.741	0.697	0.718	0.827	0.712	0.683	0.809	0.752	0.743	0.765	0.730	0.741	0.753	0.772	0.738	0.794	0.008														
PER	FCAL	0.926	0.927	0.641	0.677	0.836	0.578	0.610	0.913	0.791	0.691	0.891	0.826	0.818	0.845	0.827	0.835	0.839	0.863	0.816	0.882	0.824	0.798														
	FCOQ	0.927	0.928	0.645	0.680	0.840	0.588	0.618	0.917	0.797	0.699	0.895	0.831	0.825	0.850	0.835	0.843	0.846	0.869	0.822	0.887	0.827	0.803	0													
INT	NDIC	0.935	0.934	0.679	0.709	0.856	0.627	0.651	0.920	0.812	0.727	0.902	0.845	0.844	0.862	0.857	0.861	0.860	0.877	0.837	0.894	0.840	0.825	0.248	0.180												
	FLEN	0.928	0.928	0.640	0.677	0.846	0.590	0.624	0.941	0.811	0.702	0.914	0.843	0.842	0.865	0.870	0.875	0.868	0.893	0.840	0.910	0.834	0.813	0.250	0.344	0.536											
	NLEN	0.944	0.942	0.731	0.754	0.870	0.684	0.703	0.901	0.817	0.759	0.895	0.850	0.851	0.861	0.853	0.855	0.855	0.868	0.839	0.882	0.851	0.843	0.352	0.416	0.524	0.121										
	FCOL	0.932	0.932	0.671	0.700	0.852	0.616	0.646	0.924	0.808	0.710	0.903	0.844	0.842	0.861	0.855	0.860	0.859	0.879	0.835	0.896	0.837	0.819	0.333	0.398	0.552	0.284	0.223									
	NNIE	0.958	0.954	0.766	0.787	0.899	0.731	0.748	0.947	0.869	0.807	0.937	0.895	0.906	0.907	0.921	0.921	0.911	0.921	0.893	0.930	0.882	0.886	0.572	0.545	0.413	0.761	0.680	0.756							
	NMAU	0.933	0.933	0.701	0.726	0.846	0.636	0.659	0.867	0.783	0.722	0.863	0.818	0.811	0.827	0.803	0.806	0.814	0.828	0.800	0.846	0.826	0.808	0.087	0.183	0.359	0.225	0.306	0.309	0.537						
MAG	FPIA	0.930	0.930	0.690	0.715	0.837	0.621	0.644	0.851	0.766	0.706	0.849	0.803	0.794	0.812	0.781	0.786	0.796	0.810	0.783	0.829	0.816	0.795	0	0.024	0.141	0.229	0.310	0.318	0.354	0.070					
	NMET	0.933	0.932	0.670	0.701	0.852	0.617	0.643	0.923	0.812	0.719	0.903	0.843	0.841	0.862	0.855	0.860	0.860	0.879	0.837	0.896	0.838	0.820	0.217	0.166	0.028	0.504	0.520	0.531	0.369	0.350	0.122				
	FMET	0.923	0.924	0.620	0.659	0.831	0.553	0.585	0.918	0.784	0.673	0.891	0.821	0.811	0.842	0.824	0.835	0.839	0.864	0.812	0.885	0.817	0.788	0	0	0	0.248	0.341	0.336	0.413	0.082	0	0			
	FCHA	0.923	0.924	0.619	0.659	0.831	0.553	0.585	0.919	0.785	0.672	0.892	0.821	0.812	0.843	0.825	0.836	0.840	0.865	0.813	0.886	0.817	0.788	0	0	0	0.260	0.347	0.338	0.420	0.085	0	0	0		
	NLEC	0.933	0.932	0.670	0.702	0.853	0.620	0.644	0.926	0.814	0.722	0.905	0.846	0.845	0.864	0.860	0.866	0.863	0.883	0.840	0.899	0.839	0.823	0.224	0.162	0.099	0.532	0.538	0.560	0.390	0.375	0.149	0	0.008	0.012	



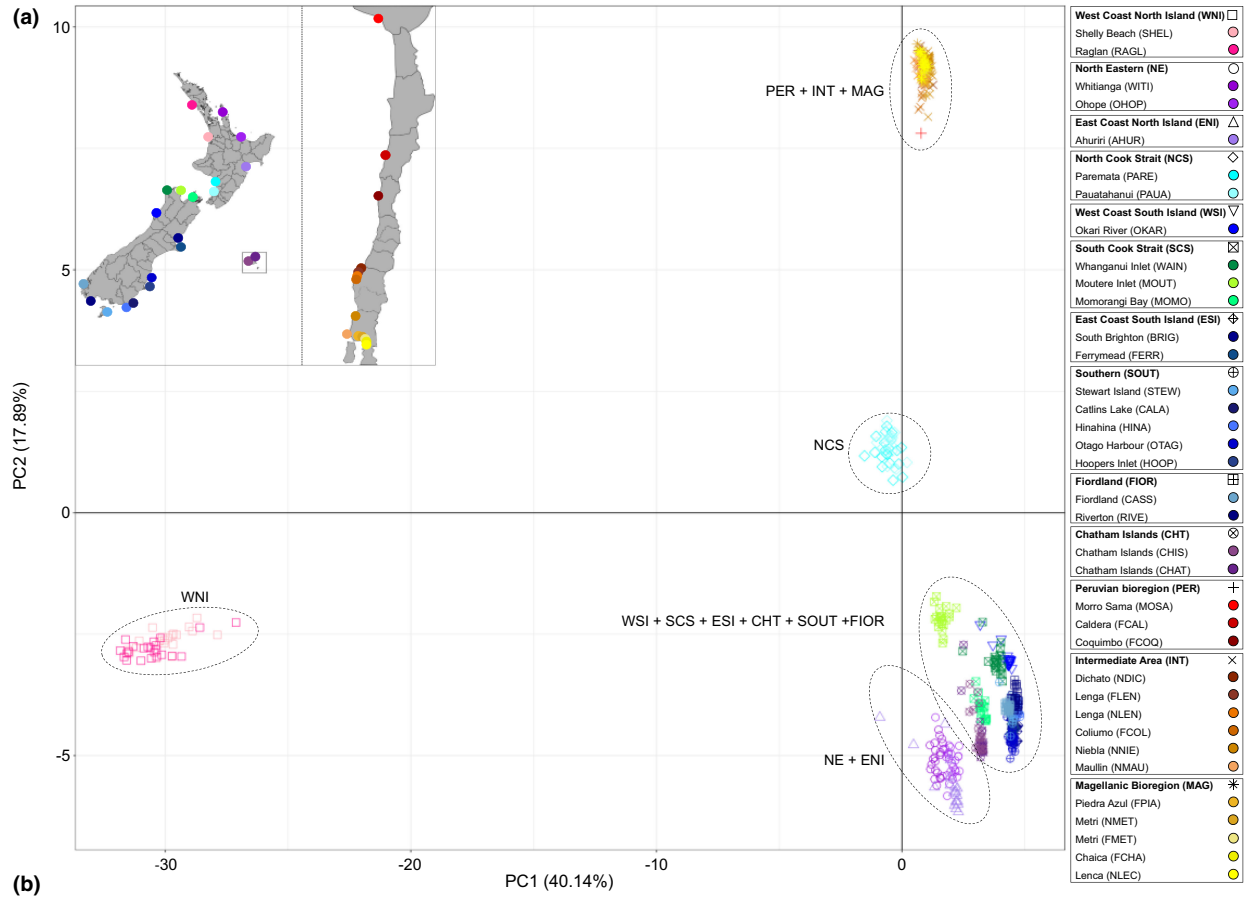
Note: Clones were not considered in the analysis and only diploid samples were used. The population of MOSA (Peru), composed only of haploids, was not included. Codes for localities are as in Table S1. Codes for bioregions are as follows: NWI = West Coast North Island, NE = North Eastern, ENI = East Coast North Island, NCS = North Cook Strait, WSI = West Coast South Island, SCS = South Cook Strait, ESI = East Coast South Island, SOUT = Southern, FIOR = Fiordland, CHT = Chatham Islands, PER = Peruvian bioregion, INT = Intermediate bioregion and MAG = Magellanic bioregion.

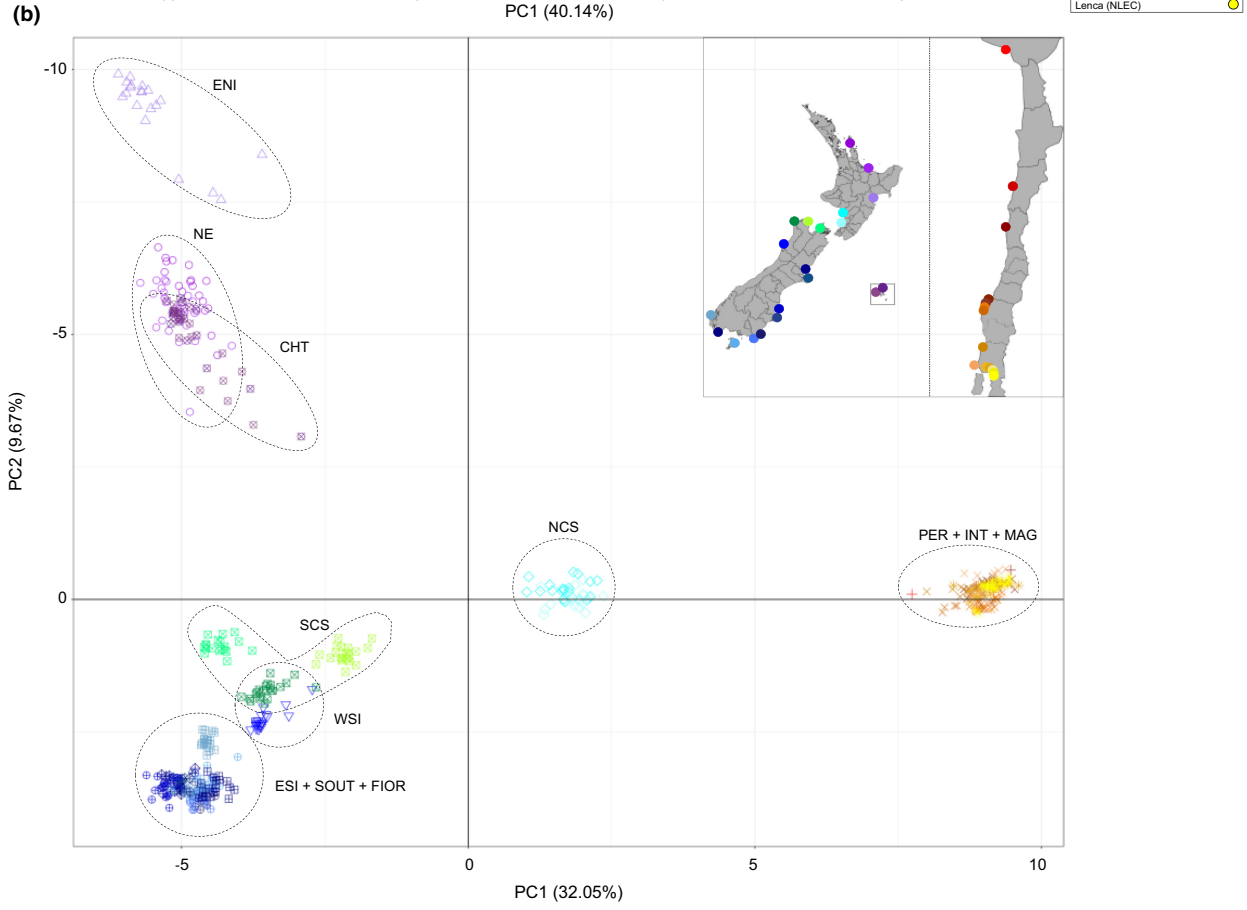
located in the West Coast North Island were clearly separated from the rest of *G. chilensis* (Figure 1). At $K = 3$, South American populations appeared as a distinct genetic cluster and populations from the North Cook Strait (i.e., Paremata and Pauatahanui) were identified as admixed between South America and New Zealand (except the West Coast North Island) (Figure 1). At $K = 4$, samples from Chatham Island, the North Eastern (i.e., Whitianga and Ohope) and the East Coast North Island (i.e., ENI, Ahuriri) were assigned to the same genetic cluster and clearly separated from the rest of the New Zealand populations (Figure 1). Populations from the North Cook Strait formed their own, nonadmixed genetic cluster at $K = 5$ (Figure 1). At $K = 6$, samples from Whitianga and Ohope were separated from Chatham Island and Ahuriri (Figure 1). At $K = 7$, the populations from the South Island were separated in two genetic clusters with one cluster located at the northwest corner of the South Island, close to the Cook Strait (i.e., Okari River, Whanganui Inlet and Moutere Inlet) and the second cluster grouping all the other populations of the South Island (i.e., from South Brighton to Riverton) (Figure 1). The two South Island populations located in between these two genetic clusters (i.e., Momorangi Bay in the northeast and Fiordland in the southwest) showed a mixed ancestry. Finally, at $K = 8$, Momorangi Bay appeared as a distinct cluster within the Cook Strait (Figure 1).

The PCA confirmed the results obtained with clustering analysis implemented in LEA. When implemented with the whole data set, the first principal component (PC) explaining 40.54% of the total variance clearly separated the populations Shelly Beach and Raglan from the rest of *G. chilensis* (Figure 2a). When excluding Shelly Beach and Raglan (Figure 2b), PC1 explained 32.05% of the variance and roughly separated South America from New Zealand, with the samples of Paremata and Pauatahanui located in the North Cook Strait showing an intermediate position. When considering only New Zealand samples (Figure S7), Chatham Island (CHT) clustered with the North Eastern (i.e. NE; Whitianga and Ohope) and appeared close to the East Coast North Island (i.e. ENI; Ahuriri).

Two major clusters were distinguished by the Neighbour-Net reconstruction, with a strong split between Shelly Beach and Raglan and the rest of *G. chilensis* (Figure 3). Twenty genetic groups, mostly corresponding to sampled localities or bioregions, were observed among the remaining populations. All South American samples clustered together and were closely related to samples from Paremata and Pauatahanui (in Figure 3 PER–INT–MAG and NCS, respectively). The cluster formed by the Chatham Island samples (CHT) showed a close relationship with the East Coast North Island (i.e., ENI; Ahuriri).

FIGURE 2 Principal components analysis (PCA) showing the clustering of *Gracilaria chilensis* samples according to the sampled locality and bioregion and implemented (a) with the whole data set, and (b) with all samples except those from the localities of SHEL and RAGL located in the Western North Island (WNI). Whatever the data set, clones were excluded from the analysis. Codes for localities and bioregions are as in Table 1 and table S1.


(a)
PER + INT + MAG
NCS
WNI
WSI + SCS + ESI + CHT + SOUT +FIOR
NE + ENI
PC2 (17.89%)
PC1 (40.14%)
10
5
0
-5
-30
-20
-10
0
West Coast North Island (WNI)
Shelly Beach (SHEL)
Raglan (RAGL)
North Eastern (NE)
Whitianga (WITI)
Ohope (OHOP)
East Coast North Island (ENI)
Ahuriri (AHUR)
North Cook Strait (NCS)
Paremata (PARE)
Pauatahanui (PAUA)
West Coast South Island (WSI)
Okari River (OKAR)
South Cook Strait (SCS)
Whanganui Inlet (WAIN)
Moutere Inlet (MOUT)
Momorangi Bay (MOMO)
East Coast South Island (ESI)
South Brighton (BRIG)
Ferrymead (FERR)
Southern (SOUT)
Stewart Island (STEW)
Catlins Lake (CALA)
Hinahina (HINA)
Otago Harbour (OTAG)
Hoopers Inlet (HOOP)
Fiordland (FIOR)
Fiordland (CASS)
Riverton (RIVE)
Chatham Islands (CHT)
Chatham Islands (CHIS)
Chatham Islands (CHAT)
Peruvian bioregion (PER)
Morro Sama (MOSA)
Caldera (FCAL)
Coquimbo (FCOQ)
Intermediate Area (INT)
Dichato (NDIC)
Lenga (FLEN)
Lenga (NLEN)
Coliumo (FCOL)
Niebla (NNIE)
Maullin (NMAU)
Magellanic Bioregion (MAG)
Piedra Azul (FPIA)
Metri (NMET)
Metri (FMET)
Chaica (FCHA)
Lenca (NLEC)


(b)
ENI
NE
CHT
NCS
PER + INT + MAG
SCS
WSI
ESI + SOUT + FIOR
PC2 (9.67%)
PC1 (32.05%)
-10
-5
0
5
10

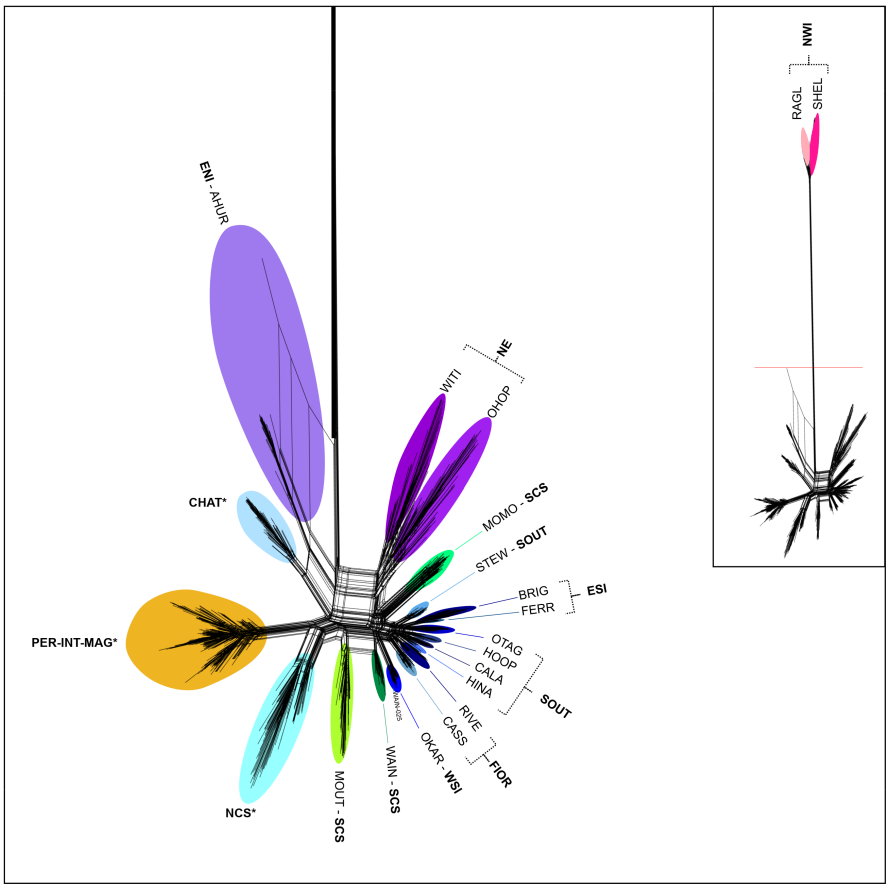


FIGURE 3 Neighbour-net network based on uncorrected distances for the 571 *Gracilaria chilensis* samples, clones excluded. Codes for localities (plain text) and bioregions (in bold) are as in Table 1 and table S1. Bioregions for which no clear subclustering by localities was observed are indicated by an asterisk.

3.3 | Inferring pathways of trans-Pacific colonization

After the first round of scenario testing in DIYABC-RF a single scenario clearly dominated the others in terms of number of votes and posterior probability within each group of scenarios (Sc3 in Group 1, Sc6 in Group 2 and Sc10 in Group 3; see Table S4 for more details). The second round of scenario testing indicated that Sc10 was the most likely of the colonization models (534/1000 votes; posterior probability: 0.77; Table S5). The lowest values of both global and local error rates were obtained for Sc10 (i.e., 0.034 and 0.23, respectively; Table S5), also supporting this model choice. Sc10 consists of two independent founder events linked to the colonization of Chatham Island from the east coast of the North Island and of Chile from the North Cook Strait (Figures 4 and S2). Parameter estimates for Sc10 had large confidence intervals and absolute errors (especially for the population size during founder events in Chile and Chatham Island, corresponding to parameters N_5b and N_4b, respectively; see Table S6). Assuming one generation every 1.5 years for *G. chilensis* (Vieira et al., 2021), Sc10 suggests that Chatham Island was colonized some 23,000 years ago while the colonization of Chile occurred 19,000 years ago (Chatham Island: t_2 median; 90% confidence interval [CI] = [23,588; 11,129]; Chile: t_1 median; 90% CI = [19,871;11,396]; Table S6). Population sizes during founder events were poorly defined but the analyses suggested that both Chatham Island and Chile experienced a strong bottleneck (Chatham Island: N_4b median, 90% CI = [7148; 30,278]; Chile: N_5b median, 90% CI = [7295; 29,671]; Table S6).

Analyses in ∂a∂i inferred a model with founder effect and complete absence of gene flow after the initial split between the Chilean and the North Cook Strait populations (best-fit model corresponded to Figure S3A; AIC = 171.23). The model suggests a population reduction of about 98% during the Chilean founder event. By contrast, the best-fit model for the colonization of Chatham Island from the North Island supported the existence of a founder effect and a constant asymmetric gene flow after population divergence (best-fit model corresponds to Figure S3C; AIC = 1145.46). The model suggests the existence of low gene flow from the North Island to Chatham Island (i.e., approximately two effective migrants per generation). The model also suggests a population reduction of 98% during the founder event in the Chatham Island.

3.4 | Testing for complex demographic history in Chile

DIYABC-RF analyses supported two alternative models for the demography of Chilean *G. chilensis*: the existence of a recent bottleneck alone (435 classification votes over 1000 RF-trees) and the existence of both an old and a recent bottleneck in Chile (485 classification votes over 1000 RF-trees; Table S7). However, the scenario supporting two bottlenecks was always the best supported

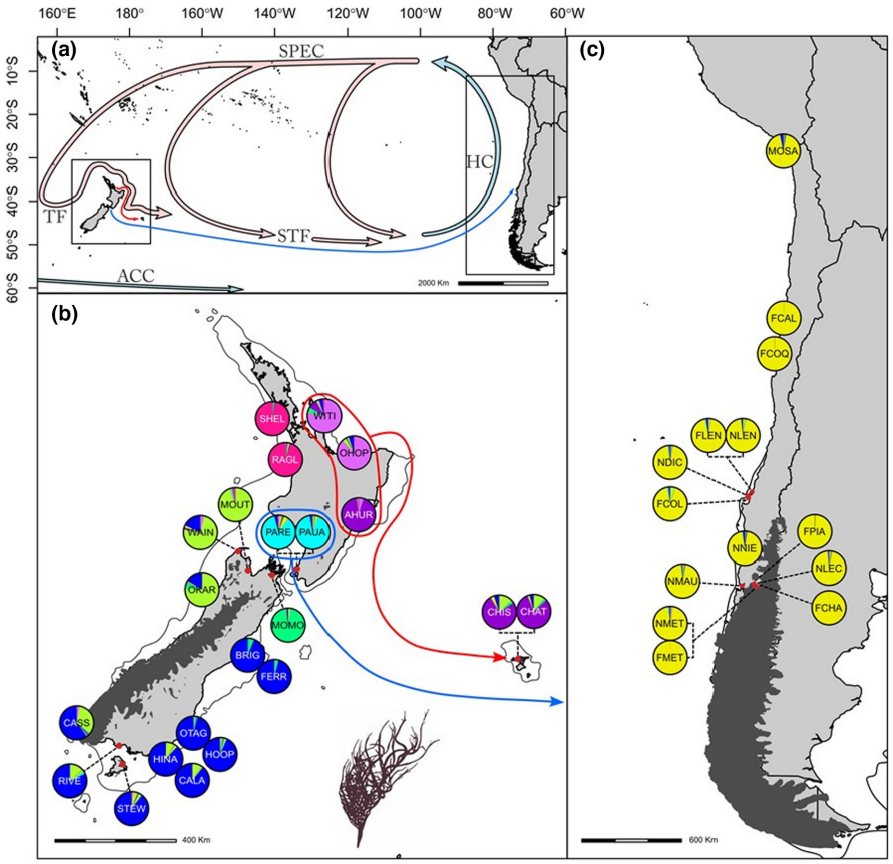


FIGURE 4 Sampling areas across the current distribution and geographical distribution of the seven genetically distinct groups of *Gracilaria chilensis*. Pie colours correspond to the population assignment results implemented using the R package LEA, assuming $K = 8$, and 2232 SNPs. The black rectangle delimits the two main sampling areas: New Zealand and South America. Codes for localities are as in table S1. The contour in fine black lines indicates the extent of the exposed shelves and dark grey shading the extent of ice during the last glacial maximum (Alloway et al., 2007; Davies et al., 2020). Prevailing currents are modified from Tomczak and Godfrey (1994) and Chiswell et al. (2015): South Pacific equatorial current (SPEC), Tasman current (TC), sub tropical front (STF), Antarctic circumpolar current (ACC) and Humboldt current (HC). Reconstructions of the most likely colonization routes followed by *G. chilensis* are shown as coloured arrows (route of colonization from New Zealand to Chatham Island in red and to Chile in blue).

through the 10 replicated analyses and it also showed the highest posterior probability (p =.431; Table S7). Scenario 4 suggests the existence of a long genetic bottleneck (i.e., 2000 generations) 23,000 years ago and a much shorter and recent one (i.e., 49 years ago, and 37 generations). The reduction in effective population size during the more recent bottleneck is much stronger than the one associated with the founder effect (effective population size during recent bottleneck: N_2r median, 90% CI = [33; 34]; effective population size during founder effect: N_2f median, 90% CI = [18,311; 29,705]; Table S8). A slow and slight increase in population size, up to two-fold, was inferred for the founder event (effective population size during founder effect: N_2f median = 18,311; posterior to the founder effect: N_2p median = 33.081). In contrast, a strong and fast demographic expansion was inferred for the recent events (corresponding to 1850-fold increase in two to three decades; effective population size during recent bottleneck N_2r median = 33; current effective population size: N_2 median = 60,948). The results should, however, be taken with caution since large 90% CI estimates and high global and local error rates were associated with all demographic bottleneck parameter estimates, reflecting poor accuracy (Table S8).

In δaδi, the 1D demographic model with the highest AIC was the constant population size scenario (AIC = 294.46). The other four demographic models had a very close fit that did not allow a clear-cut selection of the best-fit model (AIC between 154.30 and 158.22).

4 | DISCUSSION

Historical processes, especially those associated with Pleistocene climatic variations leading to genetic divergence and bottlenecks of populations isolated in glacial refugia, have shaped the genetic basis for domestication in a large number of terrestrial species (i.e., temperate species such as walnuts, peaches and apples: Feng et al., 2018, Pollegioni et al., 2017, Sun et al., 2020, Yu et al., 2018; and tropical species such as cacao and chilli pepper: Thomas et al., 2012, Scaldaferro et al., 2018). Here, we discuss three main aspects of the predomestication history of *Gracilaria chilensis*: (i) its

evolutionary history in New Zealand, its region of origin, (ii) the process of colonization of Chilean coasts and (iii) the more recent effects of harvesting and onset of cultivation.

4.1 | Evolutionary history of *G. chilensis* in its region of origin

The coastal biogeography of New Zealand is characterized by several boundaries observed in macroalgae (i.e., bull kelp species: Collins et al., 2010; Fraser et al., 2010; Laminariales: Zuccarello & Martin, 2016; and red algae: Muangmai et al., 2014, 2015, 2016), marine angiosperms (Jones et al., 2008) and benthic marine invertebrates (i.e., Schnabel et al., 2000; Stevens & Hogg, 2004; Veale & Lavery, 2011). Their location corresponds to major shifts in ocean currents, eddies and upwelling around New Zealand (Apte & Gardner, 2002; Ross et al., 2009; Veale & Lavery, 2012). Our study revealed the existence of seven genetic clusters in *G. chilensis*, mostly congruent with the described boundaries between bioregions (Ayers & Waters, 2005; Ross et al., 2009; Shears et al., 2008). The main boundaries observed in *G. chilensis* were detected around 42° S, on both the west and the east coasts. These areas are characterized by strong and regular upwelling regimes that represent important dispersal barriers due to offshore water movement (Apte & Gardner, 2002; Goldstien et al., 2006; Ross et al., 2009). The genetic discontinuity observed at East Cape, on the northeast of the North Island, separating the northernmost populations of Whitianga and Ohope from Ahuriri has been attributed to the permanent anticyclonic East Cape eddy that causes offshore displacement of the East Auckland current and contributes to gene flow restrictions (Ross et al., 2009; Shears et al., 2008; Stevens & Hogg, 2004; Zuccarello & Martin, 2016). Moreover, the convergence between the warm subtropical East Auckland current and cool northward Wairarapa coastal current may also act as an effective dispersal barrier at East Cape (Chiswell, 2001; Zuccarello & Martin, 2016).

The cluster formed by Shelly Beach and Raglan in the Western North Island was highly distinct from all other localities studied, in agreement with previous ITS2 analyses (Huanel et al., 2020). However, while the ITS2 marker detected only a moderate amount of genetic difference between the Western North Island and the rest of New Zealand, our SNPs data set supports the hypothesis of long-term complete isolation after a possible ancient introgression between populations from the Western North Island and Northern Cook Strait (see clustering analysis implemented in LEA for $K = 2$; Figure 1) that can be interpreted as ongoing speciation. Huanel et al. (2020) suggested that the Western North Island genetic cluster corresponds to a divergence pre-dating the Last Glacial Maximum (LGM). During the Pliocene, diverse tectonic and climatic changes split the North Island into a complex of small islands (Craw, 1988; Trewick & Bland, 2012), with probably limited connectivity due to sea level decrease, especially during the Pliocene–Pleistocene transition (Stevens & Hogg, 2004). These geographical changes have been related to strong population divergence in both terrestrial (Craw, 1988; Trewick & Wallis, 2001) and marine New Zealand taxa (Stevens & Hogg, 2004). Allopatric divergence may have begun during the Pliocene–Pleistocene transition and was probably reinforced by closure of the Cook Strait during the LGM (Alloway et al., 2007; Fleming, 1975), leading to complete isolation of the Western North Island.

Pleistocene glacial–interglacial dynamics also strongly affected the distribution of the genetic diversity of *G. chilensis* along the southernmost coasts of New Zealand. Indeed, the highest level of genetic diversity was observed in populations located in the North Island (i.e., particularly in the North Eastern bioregion) and in Cook Strait, while the South Island populations were characterized by low levels of genetic diversity. All highly divergent genetic clusters were also observed in the North Island and Cook Strait while South Island populations were more genetically homogeneous. This last result is confirmed by the distribution patterns of private alleles along the New Zealand coasts (i.e., higher in the North than in the South Island). The South Island, particularly its west coast, was strongly affected by the advance and retreat of ice cover during the Otira Glaciation (22,000–14,000 years ago), leading to extinction–recolonization dynamics seen in terrestrial and marine taxa (Craw, 1988, Lorrey & Bostock, 2017, Main, 1989, Stevens & Hogg, 2004,). Southern postglacial demographic expansion from one or multiple small northern refuges has been hypothesized (Buchanan & Zuccarello, 2012; Huanel et al., 2020; Marshall et al., 2009; Wardle, 1963). These results are congruent with marine paleo-evidence suggesting low temperatures at high-latitude areas, with at least 4°C less than the current average along the east coast of the South Island of New Zealand (Kohfeld et al., 2013; Lorrey & Bostock, 2017). These low temperatures suggest that the southern part of the South Island was not a suitable thermal habitat during glacial periods for *G. chilensis*, a temperate species that can tolerate temperature as low as 5°C but for which the optimum temperature for growth is 15°C (McLachlan & Bird, 1984; Usandizaga et al., 2019). Patterns of genetic diversity and structure observed with our SNPs data set suggest postglacial colonization from at least two refugia located north of 42° S, one probably located at the eastern opening of Cook Strait and the other one in Tasman/Golden Bay. Indeed, admixture in the Fiordland bioregion, a region with coastal areas highly impacted by ice scour during the LGM (Alloway et al., 2007; Craw, 1988; Lorrey & Bostock, 2017; Trewick & Bland, 2012), suggests a secondary contact of two independent recolonization fronts, one descending the east coast of the South Island and the other the west coast.

4.2 | Transpacific colonization, founder effect and genetic bottlenecks

Passive long-distance dispersal is an important promoter of range expansion and species radiations in marine organisms across the southern hemisphere (Gillespie et al., 2012; Muñoz et al., 2004). Our data show that two independent events of colonization led to the expansion of the distribution area of *G. chilensis* in the South Pacific

at the end of the Pleistocene (Figure 4). Demographic inferences estimated a colonization of Chatham Island some 23,000 years ago while the colonization of South America occurred 19,000 years ago. This is highly concordant with the estimations based on ITS2 (Guillemin et al., 2014) and with palaeoreconstructions suggesting a reinforcement of the Antarctic Circumpolar Current (ACC) for several thousand years, with an intensification of the westerly winds during glacial maxima (Kohfeld et al., 2013; Lorrey et al., 2012; Lorrey & Bostock, 2017). Wind and currents favoured a higher rate of eastward propagule transport from New Zealand's main islands to Chatham Island and South America (Kaiser et al., 2005; Lorrey et al., 2012).

Chatham Island and South American colonization events were characterized by important differences in terms of the area of origin, route of colonization, and level of gene flow between the area of origin and the newly colonized area. The colonization of Chatham Island from the North Eastern/Eastern North Island bioregions was probably facilitated by the jets and eddies (as the East Cape and Wairarapa eddies, Stevens et al., 2021) connecting to offshore main currents flowing north of the Chatham Rise (Figure 4). Similarly, genetic data supported a colonization of Chatham Island from North Island for the chiton *Sypharochiton pelliserpentis* (Veale & Lavery, 2011), the scallop *Pecten novaezelandiae* (Silva & Gardner, 2015) and the clam *Austrovenus stutchburyi* (Ross et al., 2012). On the east coast of New Zealand's main islands, both the southward subtropical East Cape Current and the colder Southland Current divert offshore when they encounter the Chatham Rise, flowing eastwards along the rise where they generate a mixture of subtropical and subantarctic waters (i.e., the Subtropical Convergence) (Barnes, 1985; Chiswell, 2005; Stevens et al., 2021). Despite their geographical isolation (i.e., 700 km), populations from the Chatham Island were remarkably genetically similar to those of the North Eastern/Eastern North Island (especially to Ahuriri), suggesting that some degree of directional gene flow occurred—and probably still occurs—from that region. Moreover, the observation of a persistent component of the South Cook Strait (i.e., South Island) in Chatham genotypes suggest some gene flow from this region may have occurred as well, leading to this apparent admixture (see Figure 1). Other studies reported frequent exchanges of migrants between mainland New Zealand and Chatham Island, these being mainly unidirectional from New Zealand to Chatham Island (Silva & Gardner, 2015; Veale & Lavery, 2011). Currently, with a 3–4 months estimated dispersal time to Chatham Island from the East Cape (Chiswell & Rickard, 2011), a low level of genetic connectivity could be ensured.

By contrast, our data suggest a single event of colonization of South America from populations located in the North Cook Strait (Figure 4), without any subsequent gene flow between the two areas. Distinct water currents could allow an eastward dispersal of marine organisms from the North Cook Strait through the South Pacific. First, the eastward D'Urville Current flows directly through Cook Strait and, second, a component of the northward Southland Current washes along the coasts of Cook Strait between Cloudy Bay and Turakirae Head (Stevens et al., 2021). Both water masses mix with the East Cape current before heading eastward (Barnes, 1985). Other studies have proposed a New Zealand origin of Chilean populations for various marine organisms, including brown macroalgae (*Adenocystis utricularis*, Fraser et al., 2013; *Durvillaea antarctica*, Fraser et al., 2009; *Macrocystis pyrifera*, Macaya & Zuccarello, 2010), red macroalgae (*Bostrichia intrincata*, Fraser et al., 2013; *Capreolia implexa*, Boo et al., 2014), green macroalgae (*Wittrockiella lyallii*, Boedeker et al., 2010) and molluscs (*Ostrea chilensis*, Foighil et al., 1999), among others. However, in contrast to *G. chilensis*, most studies on macroalgae have proposed a South Island (Boedeker et al., 2010; Boo et al., 2014) or subantarctic origin of the Chilean populations (Fraser et al., 2013; Macaya & Zuccarello, 2010). However, it has to be noted that the limited statistical power of these studies, due to the low variability of the markers, does not clearly pinpoint the area of origin of population expansion. The hypothesis of a single dispersal event is further supported by the reduced speed of the West Wind Drift, which may take up to 3 years for a 14,000-km-long rafting journey (Smith et al., 2018). Even though eastward wind can speed-up the displacement of floating rafts, such long-distance dispersal can be expected to be rare (Cumming et al., 2014; Gillespie et al., 2012; Nathan, 2006; Smith et al., 2018). However, it has been recently demonstrated that floating macroalgae can travel for years in the Southern Ocean, carrying a rich flora and fauna on their thalli over distance of thousands of kilometres (up to 25,000 km; Fraser et al., 2018).

4.3 | Predomestication losses of genetic diversity

Despite the fact that seaweed use traces back to Neolithic times (Dillehay et al., 2008) and seaweed farming is currently rapidly expanding and intensifying, many key aspects of seaweed domestication and resource management are still poorly studied (Brakel et al., 2021; Cottier-Cook et al., 2021; Valero et al., 2017). The availability of genetic diversity is a priori critical for selection to operate, and ultimately for domestication to proceed. In the case of *G. chilensis*, however, two nonexclusive processes may have driven a genetic erosion associated with the onset of farming operation: first, the collapse of natural populations that occurred in the late 1970s to early 1980s (Avila & Seguel, 1993; Norambuena, 1996); and second, the massive use of clonal propagation. Partially clonal reproduction leads to a rapid dominance of a few clones during population expansion (Rafajlović et al., 2017). In haploid–diploid organisms, this dynamic is further impacted by genetic drift during the haploid phase, which accelerates the loss of genetic diversity (Stoeckel et al., 2021). While the best-supported Approximate Bayesian Computation (ABC) scenario included both the ancient founder effect and the recent bottleneck, the scenario with only a recent bottleneck was also well supported, suggesting a strong effect of overharvesting on present-day genetic diversity. The estimated timing of the genetic bottleneck matches the onset of this over-harvesting period, further confirming its impact on the genetic diversity. ABC inferences also support a rapid increase in effective population size associated with

the expansion of farms in Chile, but the speed and magnitude of this increase seem difficult to reconcile with a simple shift in mutation–drift equilibrium. Two lines of evidence associated with farming practices may explain the observed results. First, because of the haploid–diploid life cycle, partially clonal propagation in seaweeds may lead to a rapid increase in effective population size when the population is dominated by diploids (Stoeckel et al., 2021), which is the case in *Gracilaria* farms (Guillemin et al., 2008). Second, farms are dominated by highly heterozygous genotypes, and their allelic richness does not differ from natural populations (Guillemin et al., 2008). Because ABC estimations of present-day effective population size rely essentially on the number of lineages (i.e., alleles) in the populations, the inference of a rapid demographic growth after the bottleneck could be explained by the persistence of a large number of alleles (when compared with natural populations) in these heterozygous genotypes.

The reduced genetic diversity was also associated with a reduced spatial genetic structure of the Chilean populations, when compared with New Zealand where all pairwise F_{ST} values were statistically significant and up to seven genetic clusters were detected. Some level of pairwise differentiation was observed only within the Intermediate Area, although not among all populations. One hypothesis was that farming practices, often promoting the exchange of raw material among farmers for seeding clonal fragments, could have homogenized the distribution of genetic diversity within Chile. In this case, we would expect strong genetic homogeneity among farms, but not among natural (fixed) populations, because farmed individuals are asexual and produce only a few spores, therefore limiting gene flow from farms to natural populations. Such pattern was not detected as natural populations were also poorly differentiated. Moreover, no systematic differentiation was observed between cultivated and natural populations, suggesting that farming practices did not promote a clear genetic divergence between farmed material and their wild relatives. It is therefore unclear what process led to the current distribution of Chilean genetic diversity.

Our results show that the reduced genetic diversity of *G. chilensis* in Chile results from the combined effects of the founder effect when colonizing South America, the over-harvesting during the 1970s and 1980s, and eventually the first steps of the domestication process after the establishment of farming operations. In this context, we are concerned about the status and future of *G. chilensis* domestication. As suggested earlier (Guillemin et al., 2014), these processes may be driving the species to an extinction vortex in Chile, instead of promoting its sustainable domestication. More specific assessments of neutral vs. selective processes under partial and fully clonal reproduction are required to better understand the drivers of current genetic diversity in *Gracilaria* farms, and to enable more effective management of the genetic resources. The introduction of new genetic variants in farms may be necessary to stimulate new strain selection for productive gain or pathogen avoidance. A tempting solution would be selecting these new strains from the region of origin, New Zealand, where most of the genetic diversity is present. Such an approach is being actively promoted for genetically depauperate elite cultivar populations in seaweed agronomy (i.e., Zhang et al., 2017). However, it is imperative to safeguard the eventual adaptations that the species may have evolved in the Chilean coastal ecosystems, including farming habitats, and prevent any negative impact on the quality of the Chilean genetic stock. After all, *G. chilensis* currently supports an algal industry that positions Chile as one of the principal agarophyte producers worldwide.

AUTHOR CONTRIBUTIONS

M-LG and SF conceived the study; M-LG, WAN and NA collected samples; SM, SQ-C and SM-G generated molecular data sets, with input and help from PS-A; OH, SQ-C and CRM performed the data analyses and generated tables and figures; OH, MLG, and SF wrote the original draft; and all authors edited the manuscript and approved the current version.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data are deposited in the Dryad repository: https://doi.org/10.5061/dryad.v41ns1rzw.

BENEFIT-SHARING

No benefits to reports.

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